GENERIC RECOGNITION OF BRUGMANSIA

BY

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An Historical Review

The question of whether the South American *floripondios* should be regarded as a subgenus or section of *Datura* or accorded generic rank as *Brugmansia* has long been a matter of debate among taxonomists. The precedent for their being placed in *Datura* was established by Linnaeus (14) in 1753 with the naming of *Datura arborea*. Following Linnaeus' example, Ruíz and Pavón (16), in their *Flora Peruviana* of 1799, described a new species of floripondio as *D. sanguinea* and incorrectly described another member of the genus as Linnaeus' *D. arborea*. The description of this misidentified plant was used by Persoon (15) in 1895 as the basis for *Brugmansia candida*. Persoon distinguished the two genera on differences in fruit and flower morphology as well as habit.

Persoon's treatment did not meet with universal acceptance. Bernhardi (3) pointed out in 1833 that some of the characters used by Persoon for segregating *Brugmansia* were to be found in *Datura ceratocaula*—a unique semi-aquatic species indigenous to Mexico. The "linking" characters of this species, as listed by Bernhardi,

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have been cited consistently by later taxonomists as their major reason for retaining *Brugmansia* as a section or subgenus of *Datura*. The relative taxonomic value of these characters will be discussed below.

After what appears to have been some initial uncertainty as to whether or not he should use *Brugmansia* or *Datura* in describing a new species in 1893, Lagerheim (12,13) in 1895 published a monograph of the Ecuadorean species of *Brugmansia* in which he left no doubt that he accepted Persoon's view that the two genera were morphologically distinct. Although he made several mistakes in his identifications, Lagerheim's work was the most complete study of the Brugmansias up to that time and was based on many years of field experience in Ecuador and Peru.

In his monograph, Lagerheim also drew attention to the fact that Blume's (6) use in 1828 of the name *Brugmansia* for a new genus in the Rafflesiaceae was illegitimate, because Persoon's genus in the Solanaceae enjoyed priority. Blume's use of the name *Brugmansia*, however, prompted van Zijp (20) in 1920 to propose the new generic name *Pseudodatura* for the solanaceous genus. This was done, apparently in ignorance of Lagerheim's work, because van Zijp's stated reason for proposing the new generic name was the long disuse and wide non-acceptance of Persoon's name and its new use by Blume in the Rafflesiaceae. As was pointed out by van Steenis (19), long disuse or non-acceptance by some botanists does not invalidate a name. Van Steenis agreed with Persoon and Lagerheim that the character differences between *Brugmansia* and *Datura* justified a generic separation.

More recent workers such as Safford (17), DeWolf (10), Barclay (2), Danert (9), and Bristol (7) have considered the Brugmansias as part of *Datura* following the

arguments of Bernhardi (3) that *Datura ceratocaula* forms an intermediate link between the two.

Character Differences

The primary anatomical-morphological differences between *Brugmansia* and *Datura* are listed in Table 1. Although both genera may reasonably be regarded as "weedy" plants adapted to disturbed situations and to have shared a common ancestor or ancestors, it appears from an examination of their character differences that they have evolved as a result of very different ecological pressures.

The characters that distinguish *Datura* (with the exception of *Datura ceratocaula*) are excellent examples of adaptations to a xeric environment: an annual or short-lived perennial life cycle, herbaceous habit, self-compatibility, the major part of the plant given over to inflorescence, and fruits that are dry, spiny, and dehiscent. These characters are consistent with the idea that Mexico and the southwestern United States is the center of origin and evolution of the Daturas where, during the Tertiary, they underwent rapid adaptive radiation in response to developing desert environments.

Evolving in the mesic conditions of the northern Andes, the Brugmansias retained several characters which are considered primitive relative to *Datura.* Among these characters are the bilocular ovary, self-incompatibility, and the long-lived perennial condition. It seems likely that the Brugmansias also experienced a period of adaptive radiation during the late Tertiary as the Andes underwent their last and major orogeny, opening a wealth of newly disturbed habitats suitable for invasion. Under these conditions, they developed the arborescent habit, secondary woodiness, the ability to reproduce extensively by root-suckering, pendulous flowers adapted

TABLE 1*

MORPHOLOGICAL COMPARISON OF *DATURA* AND *BRUGMANSIA*

Datura	***Brugmansia***
Habit, Growth, Form and Longevity	
Herbaceous annuals or short-lived perennials which die back to their roots.	Woody, relatively long-lived arborescent shrubs or small trees, producing vascular cylinders of considerable size.
Vegetative axes restricted to the basal portions of the plant.	The vegetative axes not limited to the basal portions.
Branching restricted to the inflorescence.	Branching not restricted to the inflorescence.
Plants lacking an effective means of vegetative reproduction.	Plants reproducing vegetatively by root suckers and forming sizable clones.
Inflorescence	
Inflorescence predominantly dichasial.	Inflorescence predominantly monochasial.
Inflorescence is localized to the upper portions of the plant, and once initiated does not revert to vegetative growth.	Inflorescence not localized and reverts to a vegetative axis at the end of flowering.
The major part of the plant is inflorescence.	The major part of the plant is not inflorescence.
Flower	
Flowers borne in an erect position.	Flowers pendulous or inclined, never erect.
Flowers closing during the day and opening in the evening.	Flowers remaining open during the day and throughout anthesis.
Anthesis one or two days.	Anthesis four to six days.
Calyx not spathe-like except in *Datura cerotocaula*, the calyx teeth usually separating more or less equally.	Calyx frequently spathe-like or split along more than one side due to the failure of the calyx teeth to separate.

* After Barclay (2) with modifications.

TABLE 1 (continued)

Flower	
Calyx circumscissile near the base and falls away with the corolla, the persistent base ultimately forming a membranous disk, cup or reflexed frill subtending the mature fruit.	Calyx not circumscissile, either falling away entirely or forming a persistent husk-like structure around the mature fruit.
Fruit	
Fruit a relatively small, dehiscent berry or capsule borne on short pedicels in an erect, suberect or nodding position.	Fruit a large pendulous berry borne on much elongated pedicels.
Bicarpellate and tetralocular due to presence of false septa.	Bicarpellate and bilocular owing to the lack of false septa.
Fruit in most species possessing a dehiscence mechanism.	Fruit lacking any dehiscence mechanism.
Pericarp usually spinose.	Pericarp smooth and unarmed.
Seeds	
Seeds relatively small and lacking a corky seed coat.	Seeds large and most species with a thick, corky seed coat.
Seeds usually with a well developed funicular caruncle.	Seeds lacking a caruncle.

to hummingbird pollination, and fruits that are large and fleshy. The derived nature of these characters would seem to preclude the possibility of *Brugmansia* being ancestral to *Datura*.

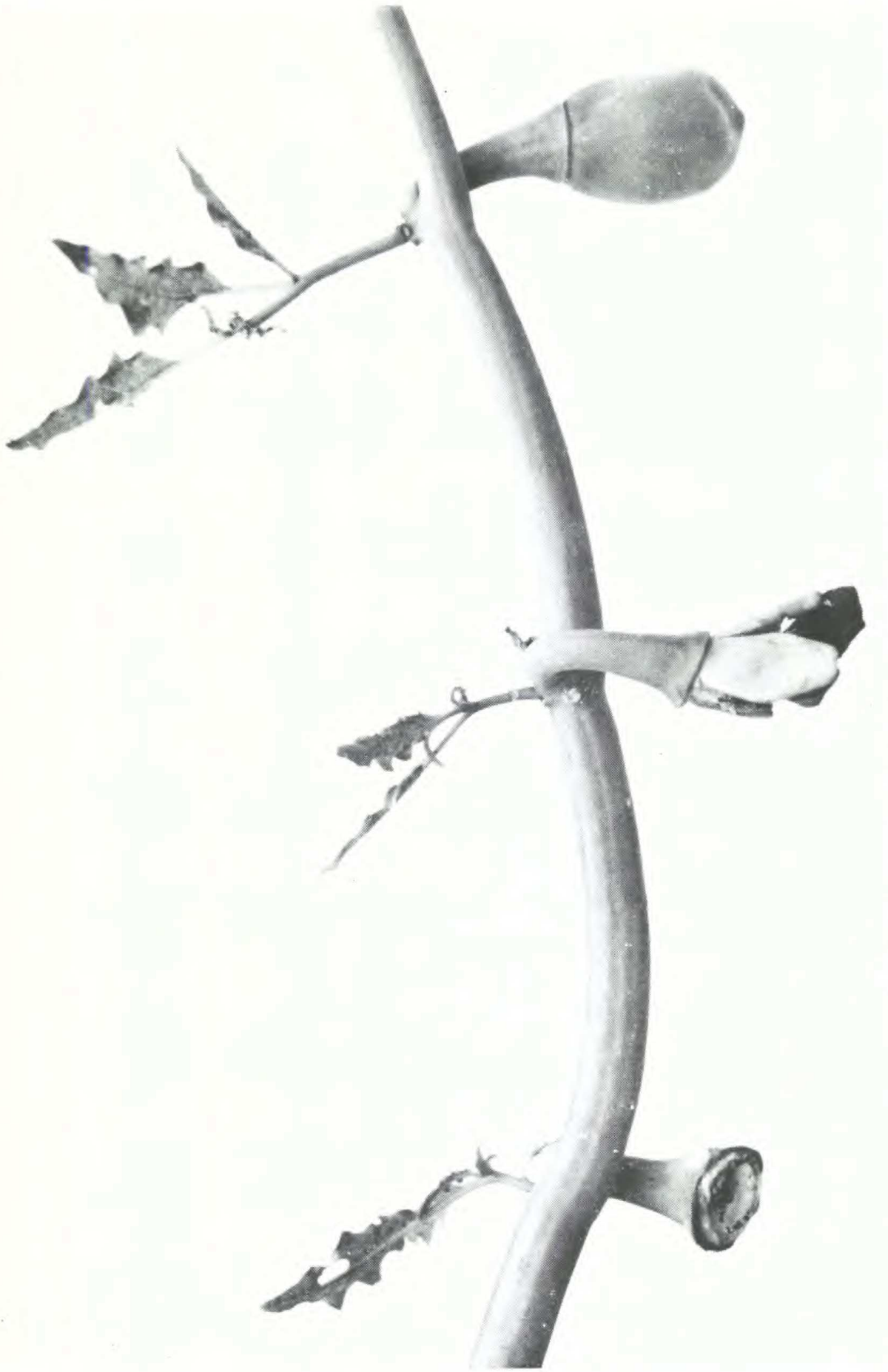
The unique combination of characters of *Datura ceratocaula* has caused Bernhardi (3), Safford (17) and others to consider it a connecting link between *Brugmansia* and *Datura*. The plant is an herbaceous annual with erect flowers, a circumscissile calyx, a tetralocular ovary, and carunculate seeds. These are all characters typical of *Datura*. It differs from other species of *Datura*, however, in having a smooth, fleshy fruit and from all other

species of both *Datura* and *Brugmansia* in being semi-aquatic.

The main character of interest is the fruit, which is essentially the "connecting link". Various taxonomists have described the fruit as a fleshy berry; as a fleshy, dehiscent berry; and as a smooth, irregularly opening capsule. Observations on plants grown in the Experimental Garden at Harvard University agree with those of Blakeslee's group (1) that the fruits are smooth, fleshy capsules which dehisce by irregular, longitudinal splitting of the pericarp into segments that curl back and break apart. It was observed also, in the cultivated plants at Harvard, that an abscission layer forms around the base of the fruit. After the initial splitting of the pericarp, this abscission layer causes the whole fruit to fall from the plant (Plate XXI). The fruits of *Datura ceratocaula* are somewhat reminiscent of the smooth-capsuled "quercina" and "inermis" mutants of *D. Stramonium;* however, they are morphologically and anatomically unrelated to the fruits of *Brugmansia*. Rather than viewing *Datura ceratocaula* as a primitive, connecting link between *Datura* and *Brugmansia*, it seems more appropriate to view it as a highly specialized *Datura*. The hollow stem, weak root system, and reduced vascular tissue are obvious specializations for its semi-aquatic habit. The possible advantages of a fleshy fruit are not as apparent; however, a dry, spiny capsule would be of less advantage here than in a xeric environment. With these specializations, *D. ceratocaula* has exploited an ecological niche unavailable to other species of *Datura* and makes it difficult to interpret them as representing primitiveness.

Due to the presence of various natural crossability barriers, it is rare to find *Datura* hybrids in the field. In the laboratory, however, most species can be hybri-

PLATE XXI



Datura ceratocaula showing dehiscence of fruit.
(*Photograph by* JAMES B. NARDI)

dized and in those cases where complete incompatibility exist, such as *Datura ceratocaula*, hybrids have been obtained by embryo-dissection and culture (5, 18). Blakeslee (4) has found that in all *Datura* hybrids the degree of fertility varies; however, all the chromosomes show a high degree of synapsis during meiosis resulting in the formation of varying numbers of closed bivalents or multivalent configurations and a complete absence of univalents. These findings led him to conclude that the differences in the genomes of the various species are due mainly to reciprocal exchanges of the ends of the chromosomes without affecting much of their structural similarity.

Even with the use of the embryo culture technique, *Brugmansia* × *Datura* hybrids are extremely difficult to produce. Carson (8) in 1945 was able to make the hybrid *Datura inoxia* (female) × *Brugmansia suaveolens*, and Joshi (11) in 1949 the hybrid *D. inoxia* (female) × *B. aurea* (this was mistakenly identified by Joshi as *B. Rosei*). In both cases, the hybrids were completely sterile. Joshi's studies showed the presence of a large number of univalents and only a few bivalents during meiosis in these hybrids. He concluded that the extremely poor synapsis in the hybrids is indicative of great structural differences in the two parental genomes.

Conclusion

The question of whether *Brugmansia* should be regarded as a distinct genus or as a subgenus or section of *Datura* has long been a matter of debate among taxonomists. Evidence based on anatomical, morphological, ecological, and genetic considerations indicates that the two have evolved independently and no intermediate or ancestral forms are known to exist. The highly specialized semi-aquatic species *Datura ceratocaula* cannot be

regarded as intermediate between the two genera, nor do the many specializations of *Brugmansia* permit it to be regarded as the progenitor of *Datura*. On the basis of this evidence, *Brugmansia* merits generic rank.

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